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Carbon burial over the last four millennia is regulated by both climatic and land-use change

Running title: Controls on millennial-scale carbon burial

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Keywords: blue carbon, carbon burial, climate change, ecosystem shift, land use change, Little Ice Age

25 **Abstract**

26 Carbon sequestration by sediments and vegetated marine systems contributes to atmospheric
27 carbon drawdown, but little empirical evidence is available to help separate the effects of
28 climate change and other anthropogenic activities on carbon burial over centennial time scales.
29 We used marine sediment organic carbon to determine the role of historic climate variability
30 and human habitation in carbon burial over the past 5071 years. There was centennial-scale
31 sensitivity of carbon supply and burial to climatic variability, with Little Ice Age cooling
32 causing an abrupt ecosystem shift and an increase in marine carbon contributions compared to
33 terrestrial carbon. Although land use changes during the late 1800s did not cause marked
34 alteration in average carbon burial, they did lead to marked increases in the spatial variability
35 of carbon burial. Thus, while carbon burial by vegetated systems is expected to increase with
36 projected climate warming over the coming century, ecosystem restructuring caused by abrupt
37 climate change may produce unexpected change in carbon burial whose variability is also
38 modulated by land use change.

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43 **Introduction**

44

45 Coastal ecosystems represent <10% of Earth biomes (Costanza & Folke, 1997) but they play a
46 disproportionately important role in the global carbon cycle (Bauer et al., 2013). Drawdown of
47 atmospheric CO₂ into the coastal ocean enables CO₂ sequestration into organic tissues by
48 photosynthesis and subsequent lock-down into sediments as sediment organic carbon (SOC)
49 (Barbier et al., 2011; Nellemann et al., 2009). This so-called blue carbon sequestration by
50 vegetated marine systems accounts for 50% of total marine C burial (Duarte, Middelburg, &
51 Caraco, 2005), with fjordic sediments accounting for at least 11% of global C burial (Smith,
52 Bianchi, Allison, Savage, & Galy, 2015), and is recognised as a potential long term store by
53 the Intergovernmental Panel on Climate Change (IPCC) (Kennedy et al., 2013). While it is
54 expected that climate warming may increase carbon sequestration by vegetated marine systems
55 (Marbà, Krause-Jensen, Masqué, & Duarte, 2018), little empirical evidence is available to help
56 separate the effects of climate change and other anthropogenic activities on carbon burial over
57 centennial time scales. Such effects include the varying influences of alteration in
58 allochthonous carbon sources, land use and climatic change (Fourqurean et al., 2012; Krause-
59 Jensen et al., 2018). For example, while in terrestrial systems modelling the impacts of land
60 use changes on carbon dynamics is increasing, in marine system climate models land use
61 change is generally excluded (Ciais et al., 2014).

62

63 Our knowledge of carbon burial by coastal systems is greatest in their quantification, largely
64 assessing marine habitats dominated by seagrass (e.g. (Duarte et al., 2005; Kennedy et al.,
65 2010; Marbà et al., 2018)), salt marshes (e.g. (Chmura, Anisfeld, Cahoon, & Lynch, 2003;
66 Kirwan & Mudd, 2012)) and mangroves (e.g. (Alongi, 2012; Bouillon et al., 2008)), SOC
67 stored in deposits created by calcifying coralline macroalgae (Trevathan-Tackett et al., 2015;
68 van der Heijden & Kamenos, 2015) and marine sediments storing allochthonous carbon
69 (Smeaton et al., 2016; Smith et al., 2015). These studies have demonstrated the comparable
70 carbon storage capacity of coastal systems to the more widely studied carbon storage
71 ecosystems on land (e.g. rainforests) (Pidgeon, 2009). This is particularly pertinent given the
72 temporal range over which many marine carbon repositories exist (centuries to millennia), and
73 thus their long-term carbon accumulation potential. Over that period, biotic activity within the
74 carbon repositories themselves can directly affect a system's capacity for carbon sequestration
75 and burial (Mcleod et al., 2011). Additionally, damage to those systems has the capacity to not

76 only prevent sequestration but also to mobilise carbon that had been previously stored for
77 millennia (Fourqurean et al., 2012).

78

79 Coralline algal ecosystems are a biodiverse habitat created by calcifying algae that support
80 multiple trophic levels (Steller, Riosmena-Rodriguez, Foster, & Roberts, 2003) and have
81 recently been highlighted as a potentially large blue carbon repository (Burrows, Kamenos,
82 Huges, et al., 2014; van der Heijden & Kamenos, 2015). Coralline algal ecosystems are
83 globally distributed (van der Heijden & Kamenos, 2015) and the accreted deposits they create
84 are stable over millennia (e.g. since the early Cretaceous (Aguirre, Riding, & Braga, 2000),
85 enabling burial and storage to occur over geological timescales. Organic carbon stored in these
86 ecosystems is predominantly allochthonous, trapped by the complex three-dimensional nature
87 of the algal thalli leading to deposit accretion (van der Heijden & Kamenos, 2015). Current
88 estimates suggest net global primary production of $173 \text{ g C m}^{-2} \text{ yr}^{-1}$ by the coralline algal
89 component of the ecosystems (van der Heijden & Kamenos, 2015), although at present little
90 empirical information is available on carbon burial and the balance between calcification and
91 burial.

92

93 Here, we investigated (1) the roles of centennial scale climate and land use change in driving
94 marine SOC accumulation and variability, (2) the longevity of carbon burial and (3) the roles
95 of ecosystem change in driving carbon burial and variability. For this we used Loch Sween,
96 Scotland, which has a well-defined land use history over several centuries (see Supplementary
97 Material), is influence by major climatic variation and sequesters and stores allochthonous and
98 autochthonous carbon in a coralline algal deposit. Sediment cores were dated using
99 radiocarbon, and isotopic composition and C/N ratios of SOC and contemporary terrestrial /
100 marine source end-members were determined to generate SOC stock, organic carbon source
101 and C/N time series.

102

103

104 **Materials and Methods**

105 **Study system**

106 The coralline algal ecosystem is a highly biodiverse habitat that supports multiple trophic levels
107 (Steller et al., 2003) and has been highlighted as a blue carbon repository (Burrows, Kamenos,
108 Huges, et al., 2014; Trevathan-Tackett et al., 2015; van der Heijden & Kamenos, 2015).

109 Coralline algal beds are globally distributed (van der Heijden & Kamenos, 2015) and are stable
110 over millennia (e.g. since the early Cretaceous (Aguirre et al., 2000)), enabling burial and
111 storage to occur over geological timescales in the sediments they trap.

112

113 **Study site and core sampling**

114 Cores (n = 3, 11 cm diameter) were collected from a live coralline algal bed in Loch Sween
115 (Figure S1), on the west coast of Scotland at a water depth of ~6 m. Core locations were spread
116 across the coralline algal bed (core 1 = nearest the loch head [86 cm core length], core 2 =
117 center of the bed [71 cm core length], core 3 = nearest the loch mouth [80 cm core length]).
118 Cores were collected using a slide hammer and SCUBA, kept in an upright position and frozen
119 immediately on return to shore (within 20 minutes of collection).

120

121 **Historic land use change**

122 Arichonan (~100 residents) was previously situated at the head of Caol Scotnish and was the
123 primary source of nutrients into the loch. It is thought to have begun as a settlement which
124 farmed livestock and grew crops in the 1600s. Major changes in habitation did not happen until
125 1848 when the population of Arichonan became largely uninhabited over the following 5 years
126 due to tenant evictions during the Highland Clearances (James, 2009).

127

128 **Age model**

129 Five new radiocarbon data points for Core 2 are presented in Table S1. Prior to radiocarbon
130 dating, suitable coralline algal thalli or shell material was selected from Core 2. For each
131 coralline algal thallus, a branch tip containing approximately 20 bands (= equivalent years of
132 growth), was selected for analysis. Shell fragments were selected as found. Surficial calcareous
133 encrustations were removed where necessary and the sample subjected to ultrasonic agitation
134 in distilled water to remove detrital particles then oven dried (40 °C). In conjunction with
135 radiocarbon dates from Core 1 (Kamenos, 2010), these new data points were used for age
136 model construction, resulting in an age record for the past 5071 calibrated years (Tables S1 &
137 S2).

138

139 Radiocarbon analysis was conducted at the NERC Radiocarbon Facility-East where the outer
140 20% by weight of sample material was removed using dilute HCl. Samples were then rinsed in
141 distilled water, dried, ground and converted to CO₂ via hydrolysis with 85% H₃PO₄. Sample
142 CO₂ was cryogenically purified and an aliquot converted to graphite via Fe/Zn reduction (Slota,

143 Jull, Linick, & Toolin, 1987). Graphite was submitted to the SUERC AMS Laboratory, where
144 sample $^{14}\text{C}/^{13}\text{C}$ ratios were determined using a NEC 250 kV SSAMS accelerator mass
145 spectrometer (Freeman, Dougans, McHargue, Wilcken, & Xu, 2008) and measured to 3%
146 counting precision.

147

148 All results were appropriately background corrected and normalised to $\delta^{13}\text{C}_{\text{VPDB}}\text{‰}$ of -25
149 according to the conventions described in (Stuiver & Polach, 1977). $\delta^{13}\text{C}$ concentrations were
150 determined using a Thermo Finnigan Delta V Duel-Inlet and are representative of the $\delta^{13}\text{C}$ of
151 the original, pre-treated sample material.

152

153 Conventional years BP (pre-1950 AD), calibrated age ranges (BC/AD) and calibrated years BP
154 are presented in Tables S1 and S2. Associated errors (one sigma) include components from the
155 counting statistics on the sample, modern reference standard, process blank and instrumental
156 error. Calibration to calendar years was conducted with OxCal version 13 (Bronk Ramsey,
157 2009) using the Marine13 (Reimer et al., 2013) radiocarbon age calibration curve. Local
158 deviations in the Marine Reservoir Effect were accounted for using a Delta-R of -47 ± 52 as
159 suggested by (Russell, Cook, Ascough, & Scott, 2015). Core tops all had live coralline algal
160 growth so were assigned a 0 years age (2015). Linear interpolation was used between dates and
161 as the oldest part of the cores contained no datable material, linear extrapolation beyond the
162 dated range was also used to estimate their age.

163

164 The ^{14}C age model was further tuned using magnetic susceptibility (MS) performed on all core
165 horizons (Figure S2). Direct measurements of MS (Bartington MS3E, 3.8mm spatial
166 resolution, e.g. (Peti & Augustinus, 2019; van der Bilt et al., 2018)) were made on the flat
167 surface of core horizons at the central portion of the core. The horizon surface was tightly
168 covered by a single layer of plastic film during the measurement to prevent sensor
169 contamination. Six contiguous measurements were taken on each horizon and considered as
170 averages \pm SD. The sensor was calibrated after each measurement following manufacturer
171 specifications.

172

173 **End-member sampling for isotopic calibration**

174 End member samples were collected at the sample site to enable fingerprinting of the SOC
175 source. These included: soil (up to 15 cm depth, $n = 5$ along an altitude gradient from the shore),

176 terrestrial plants common to the area (7 species, Table S3), partially degraded leaves found
177 within the coralline algal bed (only *Quercus petraea* leaves were found), water column
178 particulate organic matter (POM) (0.2 μm seawater filtrate, n = 5), marine macroalgae (10
179 species, see Table S4) and marine invertebrates (4 species, Table S3). Terrestrial samples were
180 frozen immediately on collection. Marine macroalgae were gently cleaned following
181 collection, rinsed with deionized water and frozen. Marine invertebrates were depurated in
182 filtered seawater for 12 hours following collection, before being rinsed with deionized water
183 and frozen.

184

185 **Sample preparation**

186 Each sediment core was cut into 2cm horizons whilst still frozen. Each horizon was then dried
187 at 60°C for three days and sieved into three size fractions for subsequent SOC analysis (<63
188 μm , 63-250 μm , 250-500 μm). Each fraction was ground into a fine powder using a ball mill
189 and a small portion was acidified (5N HCl). Carbonate specimens (e.g. fragments of shell or
190 coralline algae) were picked from the >500 μm fraction for ^{14}C dating (described above). All
191 isotopic end member samples were oven dried at 60°C for three days and ground into a fine
192 powder. Half of each powdered sample was then acidified to remove carbonate material (5N
193 HCl), before rinsing with deionized water and drying for a second time.

194

195 **Stable isotope analysis**

196 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope analyses was conducted at the NERC Life Sciences Mass
197 Spectrometry Facility (at SUERC) to identify the primary source(s) of organic matter in each
198 sediment horizon. This enabled discrimination between terrestrial / marine inputs and trophic
199 levels via comparison to the end member samples (e.g. (Graham, Eaves, Farmer, Dobson, &
200 Fallick, 2001; Macreadie, Allen, Kelaher, Ralph, & Skilbeck, 2012; Thornton & McManus,
201 1994)). Since marine organisms are distinctly less cellulosic but more proteinaceous than
202 terrestrials, C/N ratios have also been widely used for reflecting physical mixing of sediment
203 material composited by distinct end member sources. A marine algal dominated source of
204 sediment material is represented by C/N ratios of 4-10 (Meyers, 1994); C/N ratios >12
205 represent terrestrial vascular plant end member sources (Lamb, Wilson, & Leng, 2006). All
206 analyses were carried out using a Delta Plus XP continuous flow isotope ratio mass
207 spectrometer (Thermo Fisher Scientific, Bremen, Germany) coupled to a Pyrocube Elemental
208 Analyser (Elementar, Langenselbold, Germany). Three laboratory standards (Gelatin,
209 Alanine/Gelatin and Glycine/Gelatin) were analysed for every 10 unknowns and used to

210 correct for instrument drift during each analytical run, which typically lasts 16 hours. Four
211 aliquots of USGS50 were analysed each day (average and standard deviation for USGS 40 over
212 6 analytical runs, spanning a period of 6 months (n=24) was $\delta^{13}\text{C}$ -26.35 +/- 0.13‰ and $\delta^{15}\text{N}$ -
213 4.60 +/- 0.20‰, accepted values are -26.39 +/- 0.04‰ and -4.52 +/- 0.06‰ respectively).
214 While $\delta^{13}\text{C}$ analyses were possible for all sediment fraction sizes, only the <63 μm fraction had
215 sufficient N to accurately determine $\delta^{15}\text{N}$. SOC mass was quantified via weight percentage of
216 organic carbon (OC%) and total carbon (TC%), determined by mass spectrometry.

217
218 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were determined in each 2 cm horizon of core 1, providing a 20-40 year
219 resolution. For cores 2 and 3, analytical limitations prevented analysis of all the horizons: from
220 860-150 calBP 20-40 year resolution was achieved, while horizons older and younger than this
221 period were analysed at up to ~180 year resolution (Table S2).

222

223 **In situ seawater temperature**

224 A fortnightly 653-year reconstructed in-situ water temperature (IST) record for Loch Sween is
225 available from Kamenos (2010), enabling a direct comparison between IST and carbon storage
226 at the same location.

227

228 **Calculation of C stock**

229 Areal carbon storage (Mg Ha^{-1}) was quantified using weight % organic carbon (OC), the mass
230 of the horizon and the core surface area:

231

$$232 \quad \text{SOC}_{\text{stock}} = \sum_i S_i \times A$$

233 where, i refers to the three fractions of sediment, S_i is total SOC stock, and A is the core surface
234 area. The SOC stock of each horizon was calculated as:

$$235 \quad S_n = WT_n \times W_n$$

236

237 where, n refers to the core horizon, WT is the weight percent of OC in each horizon, and W is
238 the total mass of each horizon.

239

240 **Statistics and isotopic mixing model**

241 Data analysis was conducted in R (version 3.3.2: One-way ANOVA and Pearson correlation
242 coefficient). The segmented package (Muggeo, 2008) was used for breakpoint regression

243 analysis, the Stable Isotope Analysis in R (SIAR) mixing model package (Parnell, 2013) for
244 stable isotope mixing models and ggplot2 (Wickham, 2010) for visualizing data. Cross-wavelet
245 coherence analysis was used to describe time series and compare marine in situ temperature
246 with carbon metrics; analyses were conducted in R using the WaveletComp package (Roesch
247 & Schmidbauer, 2014).

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250

251 **Results**

252 Both organic carbon (OC) and total carbon (TC) showed a decreasing trend from the present
253 day to ~400 calBP (Figure 1), accompanied by a distinct diversion of OC and TC during the
254 period 400-250 calBP. As would be expected, a degree of SOC remineralisation was observed
255 (indicated by a general decline in OC over time): this was apparent for the last ~400 years,
256 prior to which the quantity of buried organic carbon stabilized to a constant, but lower,
257 concentration.

258

259 While there is little evidence of a change in mean TC and OC directly after 1848 (~125 calBP),
260 when the local habitation and livestock husbandry at Arichonan ended abruptly, there is a
261 notable increase in OC standard deviation during the period ~1848-1950 calAD (~125-0
262 calBP). Both TC and OC both show a marked narrowing of SD in ~125calBP (1848-50 calAD)
263 and also ~420 calBP (~1625 calAD) (Figure 1). While these relatively short periods of reduced
264 SD are do not directly link with troughs in IST (Figure 1), there is evidence of wider coherence
265 between IST and OC as well as inorganic carbon (IC) and TC with a 65y period between 320-
266 220 calBP and 150-0 calBP, and a 150y period from 250-150 calBP ($P < 0.05$).

267

268 **Temporal change in the source of organic carbon**

269 The baseline end members provide a distinction between marine / terrestrial inputs, and across
270 trophic levels (Figure 2). The $\delta^{13}\text{C} / \delta^{15}\text{N}$ composition of the sediment fell into two discrete
271 temporal periods (Figure 2); this temporal change was consistent across all cores. Prior to ~370
272 calBP, the organic matter was characterised by lower $\delta^{15}\text{N}$ (<6.0‰, Figure 2) and there was
273 evidence of higher C/N elemental ratios (increased SD) (Figure 3) typical of terrestrial C3
274 plants, suggesting that terrestrially-derived carbon was an important component of the total
275 organic carbon pool in this system until ~370 calBP (macroalgal-derived organic material

276 (40%), terrestrial plants (28%), terrestrial soil (21%) and marine fauna (11%) (Figure S5)).
277 $\delta^{15}\text{N}$ during this period remained relatively constant. In contrast, sediments deposited more
278 recently than ~370 calBP were characterised by higher $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ typical of marine algae
279 and fauna (Figure 2) and C/N elemental ratios were also indicative of marine-derived sources
280 (Figure 3), suggesting a recent transition towards a dominance in marine-derived organic
281 carbon (marine fauna (~42%), macroalgae (~27%), terrestrial plants (~24%) and terrestrial soil
282 (~8%) (Figure S5)). Additionally, more recently than 370 calBP $\delta^{15}\text{N}$ was characterised by a
283 significant increase over time ($F_{1,40}=30.1$, $p<0.001$; Figure S4), suggesting a temporal increase
284 in the proportional contribution of higher trophic levels to the carbon stored (i.e. derived from
285 marine consumers, e.g. marine invertebrates). $\delta^{13}\text{C}$ variation showed a general increase over
286 time ($F_{1,71}=105.9$, $p<0.001$; Figures 2 & S3), but no clear temporal groupings in the dataset
287 were observed. The major change in isotopic composition during ~370 calBP occurred directly
288 after the marked drop in the in-situ temperature, but at least 200 years before the major change
289 in habitation at Arichonan during 1848 (Figure 1). Partially degraded leaves found in the
290 coralline algal bed were enriched in $\delta^{15}\text{N}$ compared to their terrestrial counterparts although
291 they still remained in the 'terrestrial' envelope. Water column particulate organic matter lay
292 between the marine-derived and terrestrially-derived inputs (Figure 2).

293

294 **Bulk carbon stock**

295 Organic carbon in coralline algal systems is associated primarily with the SOC buried in the
296 open matrix carbonate deposits that are created by the calcifying organisms (van der Heijden
297 & Kamenos, 2015). Within the upper 25 cm of sediment, 7.23 ± 1.30 (mean \pm SD) Mg OC Ha⁻¹
298 were stored in the coralline algal bed (Figure 4). This is similar to temperate Australian
299 seagrasses (Lavery, Mateo, Serrano, & Rozaimi, 2013) but is higher than estimates for high
300 latitude kelp forest standing stock (1.41 ± 0.66 Mg C Ha⁻¹) (Burrows, Kamenos, Hughes, et al.,
301 2014) and the average for high latitude marine sediments (2.51 ± 2.1 Mg C Ha⁻¹) (Burrows,
302 Kamenos, Hughes, et al., 2014). Across the full depth of the cores, the total organic carbon
303 (TOC) stock of the coralline algal bed was 12.28 ± 1.98 Mg OC Ha⁻¹. Thus, ~60% of the TOC
304 stock was stored in the top 25 cm of the deposit.

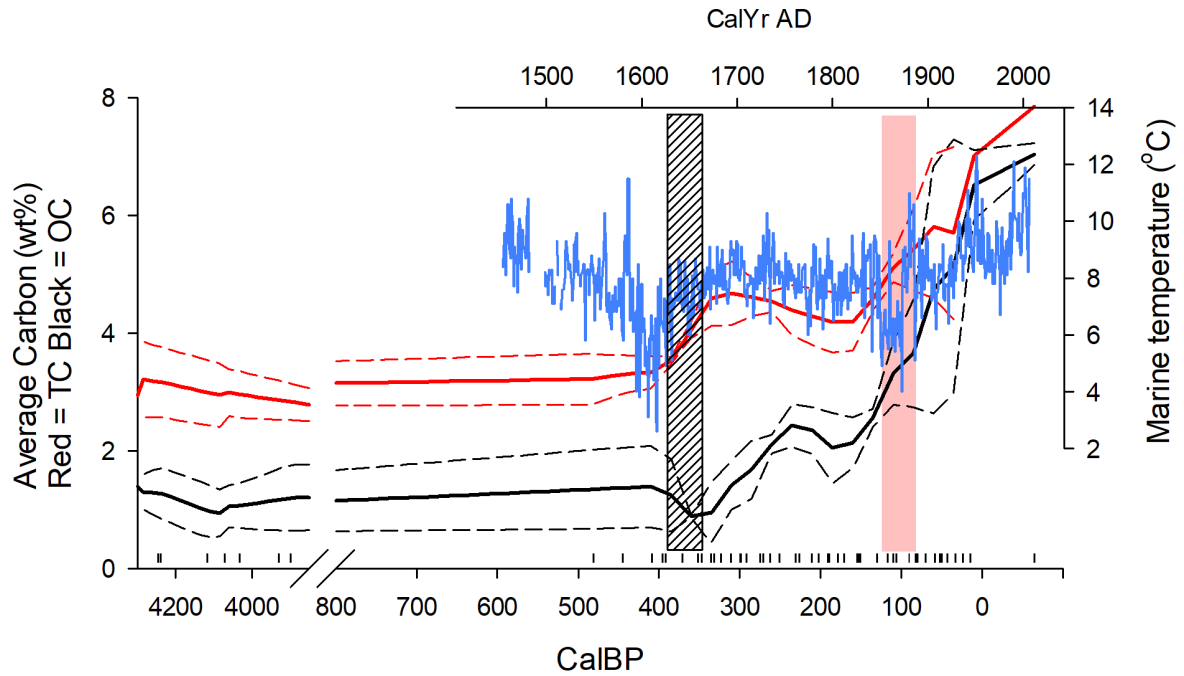
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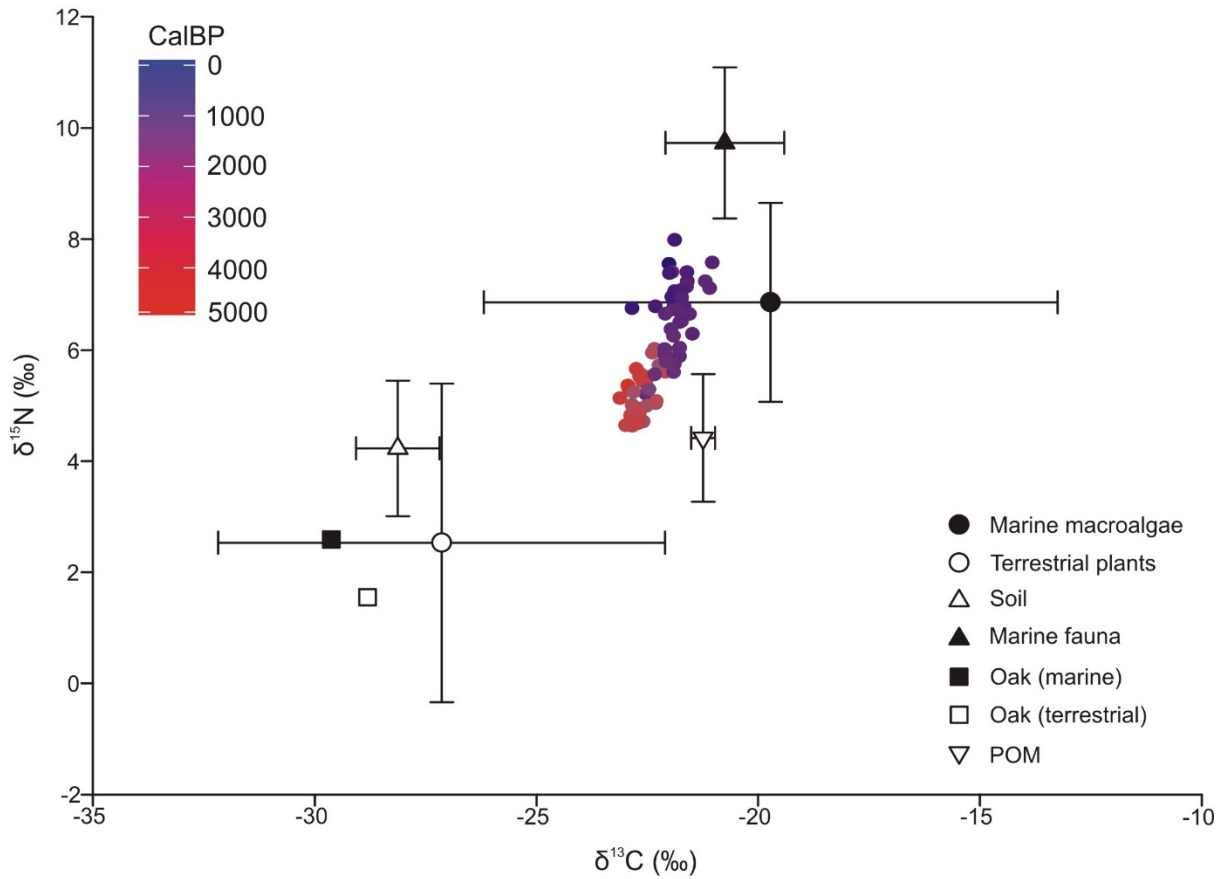
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313 **Figure 1** Average total carbon (TC, red line, n = 3 per time point), organic carbon (OC, black
314 line, n = 3 per time point) and marine temperature (blue line). Dashed lines represent SD.
315 Vertical rug on x axis defines calBP age of each core section used in TC and OC determination.
316 Blue line represents in situ reconstructed marine temperature of the sampling site (Kamenos,
317 2010). Black diagonal shading indicates period of proposed ecosystem reorganization (from
318 Fig 2). Red shading indicates timescale of abrupt land use change.

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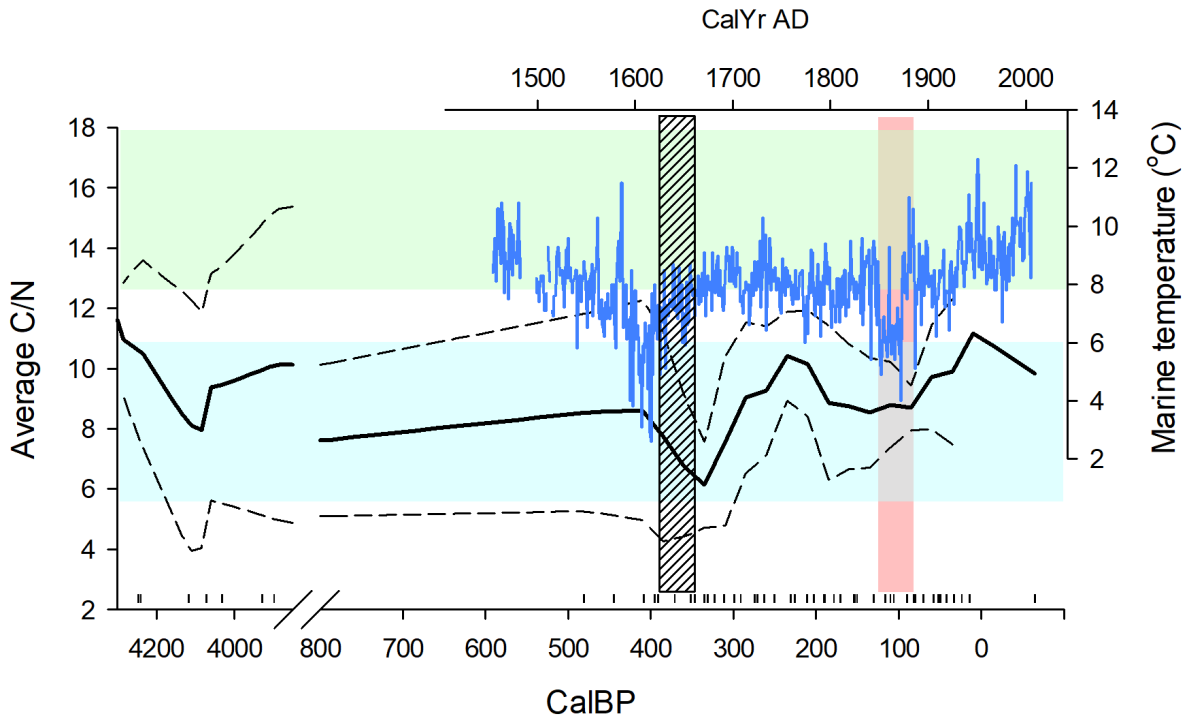
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323 **Figure 2** $\delta^{13}\text{C}$ against $\delta^{15}\text{N}$ (‰) of core organic material (<63 μm size fraction, coloured points,
 324 colour-coding = sediment age) and end-members (black/white symbols, mean \pm SD). ‘Oak
 325 (marine)’ refers to fallen oak leaves that were collected underwater from within the coralline
 326 algal bed framework. Oak was represented by 1 terrestrial and 1 marine sample so no SD
 327 presented. POM = particulate organic matter.

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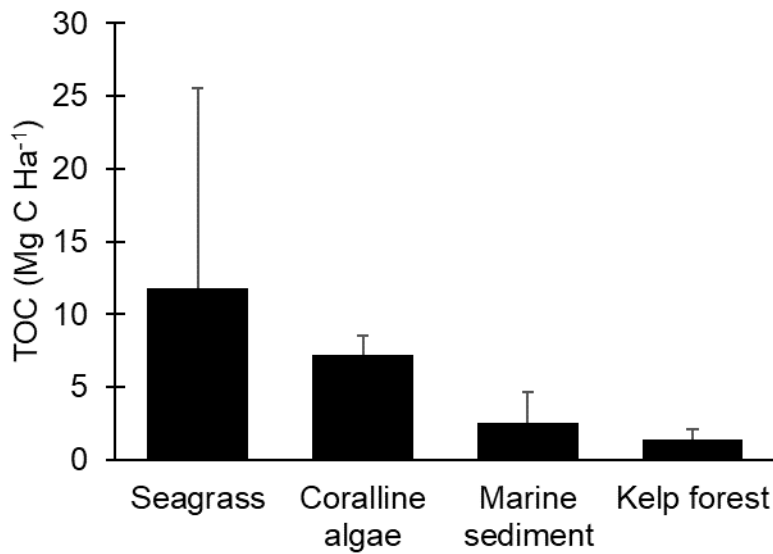
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Figure 3 Soil organic material C/N elemental ratio (mean (n = 3 cores; solid line) ± SD (dashed lines)) and marine temperature (blue line; from Kamenos (2010)) over time. Vertical rug on x axis defines calBP age of each core section used to calculate C/N. Blue horizontal shading represents typical marine algal C/N ratios as defined in (Meyers, 1994). The green horizontal shading represents typical terrestrial plant C/N ratios, as defined in Lamb et al (2006). Black diagonal shading indicates period of ecosystem reorganization (from Fig 2). Red shading indicates timescale of abrupt land use change.

340



341

342 **Figure 4** Sediment organic carbon stock (TOC Mg C Ha⁻¹) in systems classified as blue carbon
343 repositories. Average concentrations (+SD) for top 25 cm of seagrass mats, including above-
344 ground biomass (Lavery et al., 2013), the top 25cm of coralline algal deposits (this study) and
345 top 25 cm of marine sediment (Burrows, Kamenos, Hughes, et al., 2014), and above-ground
346 kelp biomass standing stock (Burrows, Kamenos, Hughes, et al., 2014).

347

348

349 Discussion

350

351 Here we show evidence of the influence of both historic temperature and land use changes on
352 carbon accumulation at centennial time scales. The distinct period of low OC accumulation
353 (starting ~370 calBP) directly followed the onset of environmental cooling during the mid-LIA
354 temperature minimum (e.g. (Asteman, Nordberg, & Filipsson, 2013; Cage & Austin, 2010;
355 Kamenos, 2010)), while wide variability in OC burial follows major land use changes after 125
356 calBP.

357

358 Climate and land-use regulation of carbon burial

359 The coherence between OC and historic temperature variability may be driven by a decrease
360 in organic production during periods of reduced temperature because of (1) a decrease in the
361 metabolic rates of marine organisms (Nwewll & Northcroft, 1967) and / or (2) reduced
362 terrestrial runoff during cooler phases, reduced nutrient delivery to marine systems and a

363 subsequent reduction in primary productivity (Szczuciński, Zajączkowski, & Scholten, 2009).
364 This is supported by the abrupt change in the source of organic matter around ~370 calBP
365 (Figure 2), characterised by a rapid increase in the proportional dominance of marine-derived
366 matter and a reduction in terrestrially-derived matter. It is possible that the biological pathways
367 linking carbon burial and climate coherence at 65y and 150y periods differ; those driving 65y
368 period coherence being sensitive to temperature reduction while those at 150y period breaking
369 down at higher temperatures seen during the last century (Figure 1).

370

371 Our data suggests a large, climate-driven, ecosystem shift that occurred at ~370 calBP,
372 supported by three lines of evidence: (1) an abrupt increase in the proportion of carbon from
373 higher trophic levels in younger sediments (Figures 2 & 3), (2) an increase in the contribution
374 of marine-derived matter to the carbon stock in younger sediment, compared to a higher
375 dominance of terrestrially-derived matter in older sediment (Figures S5) and (3) absence of a
376 dramatic change in sediment composition (Figure S2), indicating that (1) and (2) happened
377 locally and were not due to a new source of organic material derived at distance from the site.
378 Disturbance and reorganization of ecosystems due to temperature changes are known in marine
379 ecosystems (Gutierrez et al., 2009) and, more widely, in terrestrial ecosystems (Nolan et al.,
380 2018); these changes can involve replacement of dominant organisms / functional types and be
381 accelerated by other interacting processes (Hughes et al., 2007; Overpeck, Rind, & Goldberg,
382 1990). Our data suggest that the ~370 calBP LIA-triggered ecosystem shift was associated with
383 a relative decrease in marine productivity followed by an increase in productivity (excluding
384 the longer-term trend driven by background remineralisation, Figure 1), further supported by
385 the C/N ratios which become more marine after the temperature minima during the LIA (Figure
386 3). This may be associated with a shift to a larger proportion of calcifying biota (other than the
387 coralline algae themselves), evidenced by the divergence in TC and OC beginning around 400
388 calBP. Notably, there is a ~50 year lag between the change in climate and the peak of ecosystem
389 restructuring; such lags in response to climate change have also been recorded in other
390 terrestrial and marine ecosystems and can be related to variable sensitivities of different parts
391 of the ecosystem and associated interacting factors including population size, dependence on
392 prey availability and resource competition (Camill & Clark, 2000; Poloczanska et al., 2016).
393 In Caol Scotnish, this lag may be further enhanced by such interacting ecosystem processes
394 occurring in both terrestrial and marine sources of organic material.

395

396

397

398 Just after the 125 calBP (1848-50 calAD) cooling period, OC standard deviation abruptly
399 increased, reaching the largest SD in the record, until 0 calBP (~1950 calAD) before gradually
400 reducing to 2015. We interpret this widening of responses as divergent influences of climate
401 and land use changes due to human habitation on carbon burial. In 1848 the village of
402 Arichonan (the primary source of anthropogenic inputs to Caol Scotnish) was abandoned
403 abruptly during the Scottish Highland clearances, leaving the farmed land to rewild from its
404 previous use in animal husbandry and arable agriculture. Our data suggest land use changes
405 led to markedly variable organic carbon inputs, possibly due to changes in runoff patterns and
406 the source of allochthonous carbon. This caused increased heterogeneity in carbon burial while
407 not necessarily changing the mean quantity of carbon buried. Further, a component of that
408 increased variability may be caused by subtly different rates of temporal organic carbon
409 breakdown and remineralisation across the coralline algal bed during that period. Although
410 there are two distinct periods of very reduced SD in TC and OC, these are not consistently
411 associated with distinct climatic patterns so, given the number of replicate cores (n=3), we
412 attribute them to chance.

413

414 In this system, land use change to farming was gradual, followed by abrupt rewilding.
415 However, there is evidence that where habitats are damaged, losses of carbon from vegetated
416 wetlands can be linked to eutrophication (e.g. wetlands (Hopkinson, Cai, & Hu, 2012)),
417 dredging (seagrass (Greiner, McGlathery, Gunnell, & McKee, 2013)) as well as natural
418 disturbances for exposed repositories including hurricanes (e.g. mangroves (Barr, Engel,
419 Smith, & Fuentes, 2012)). Although we have little empirical evidence available for specific
420 changes in land use during the period over which Arichonan was inhabited, the notable drop in
421 carbon burial during 180 calBP – at which time there is no obvious thermal driver – may be
422 due to negative changes in land use practices. Such variability in carbon release caused by
423 changes in land use, and the way this is modelled, is a driver of differences between climate
424 models, but this currently is not well integrated into marine modeling approaches (Ciais et al.,
425 2014).

426

427 **Role of calcifying algal systems in carbon burial**

428 Relatively little is known about the role of calcified ecosystem engineers in carbon burial,
429 where a balance exists between carbon burial and biological processes that release carbon (e.g.
430 calcification) (van der Heijden & Kamenos, 2015). Organic carbon in these systems is

431 associated with both the calcifying engineer and associated SOC buried in the carbonate
432 deposits that are created by the calcifying organisms. Here we have shown that the quantity of
433 SOC buried in deposits created by calcified vegetated ecosystem engineers is comparable to,
434 if not higher than, other vegetated systems. As would be expected, a degree of SOC breakdown
435 and remineralisation was observed (as a general decline in OC over time). However, this was
436 apparent for only ~500 years, after which the quantity of buried organic carbon stabilised.
437 Importantly, coralline algal ecosystems are found throughout the world's coastal ocean, from
438 the intertidal to 100+ m depth and their deposits are frequently stable for millennia (van der
439 Heijden & Kamenos, 2015), representing a globally significant carbon store relevant at
440 geological timescales. Our results show that this coastal vegetated system has persisted for at
441 least the past 5070 years, and despite abrupt ecosystem shifts during this time, has been actively
442 burying and storing blue carbon for the duration.

443

444 Calcifying algae can also be significant components in other vegetated systems. We now know
445 that seagrass meadows, which are recognised blue carbon storage ecosystems (Fourqurean et
446 al., 2012), are also globally significant 'hotspots' of calcium carbonate production because of
447 the abundance of calcifying organisms such as epiphytes (including red coralline algae),
448 benthic invertebrates, carbonate deposition during sedimentation, and direct carbonate
449 formation by some seagrass species (Mazarrasa et al., 2015). Despite this potentially large
450 source of CO₂ release via the calcification process, seagrass meadows likely still exhibit a net
451 drawdown of CO₂ (Macreadie, Serrano, Maher, Duarte, & Beardall, 2017), demonstrating that
452 high carbonate production does not preclude an ecosystem's role in net blue carbon storage.
453 Thus, we suggest that calcifying algal systems may in fact represent a substantial, global-scale
454 blue carbon repository with millennial longevity. We have shown that this carbon burial
455 potential is sensitive to climatic variability (and subsequent biogeochemical effects) at multiple
456 scales, including long-term climate trends, local ecological structure (e.g. terrestrial and marine
457 primary production) and hydrogeology (e.g. sediment dynamics, river discharge).

458

459 **Conclusions**

460 We suggest that the quantity and variability of carbon burial is dependent upon the stability of
461 ecosystems and their associated organic production. That relationship can be particularly
462 complex because of the varied factors that can influence ecosystem structure, including
463 climatic variability and, more recently, direct human impacts such as land use change and
464 increased nutrient run-off, which can result in an increase in carbon efflux (e.g.

465 remineralization) (Macreadie et al., 2012). However, at centennial scales (the time scale over
466 which significant amounts of carbon can accumulate) major changes in climate drives
467 ecosystem structure and carbon burial, while land use change appears to increase the variability
468 of carbon burial. The projected 2-4°C warming over the 21st century (IPCC, 2013) would
469 intuitively be expected to lead to an increase in the quantity of carbon buried over coming
470 decades, driven by concurrent increases in metabolic activity and ecosystem production.
471 However, we suggest that such responses will likely be complicated by (1) changes in other
472 environmental parameters (e.g. carbonate chemistry, oxygenation) projected for the end of the
473 century (IPCC, 2013), (2) land use changes which could cause large variability in carbon burial
474 and (3) rapid projected warming which may cause similar ecosystem reorganisation to that seen
475 during the rapid cooling of the LIA, leading to reduced organic carbon supply despite higher
476 productivity.

477

478 **Data Sharing and Data Accessibility**

479 Data used in this manuscript are available at DOI:10.17632/hgkwvww43z.1

480

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486

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